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Perakanthus (Rubiaceae-Vanguerieae), a rare Malay Peninsula endemic: generic delimitation, status and affinities

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Summary. The character states of *Perakanthus velutinus* (morphology, anatomy, reproductive biology: secondary pollen presentation, palynology and karyology) are described. Comparison with the second species originally described in the genus, *"P." pauciflorus*, confirmed that its exclusion from the genus by Wong (1989) was justified. A formal emended generic description is included and the genus is formally typified. Comparison with other Asiatic members of the tribe Vanguerieae, hampered by the ill-known state of most genera and, in part, uncertain generic delimitations, suggests that *Perakanthus* may have its closest affinities with *Canthium sensu lato* (excluding *Psydrax* and *Pyrostria*), so that its status as a monotypic genus remains to be confirmed. Detailed investigations of the entire Asiatic Vanguerieae complex, including molecular studies, are required to solve this question.

Perakanthus Robyns is a rare forest genus endemic to the Malay Peninsula. After removing one of its species (Wong 1989), *P. velutinus* remains the only representative of the genus. Good flowering and fruiting material collected and preserved in 2004 in Endau Rompin National Park provided a good opportunity to thoroughly study the taxon's character states. With a complete overview of its characteristics available, it was also possible to recheck *P. velutinus* against the second species originally associated with *Perakanthus*, and to attempt a clarification of the status of *Perakanthus* and to discuss its affinities within the tribe Vanguerieae.

MATERIALS AND METHODS

All detailed investigations on *Perakanthus velutinus* were carried out on preserved material of *Puff* 040402-1/1 (Malay Peninsula, Johor, Endau Rompin National Park, around Kuala Marong rest area, 02 April, 2004, buds, flowers and fruits); the corresponding herbarium voucher is *Zahid* et al. ZMS 31, deposited at KLU.

Anatomical studies were partly carried out on thin hand sections and partly on microtome sections (preparation and methods as in Igersheim 1993). Pollen was investigated under the light microscope only. Chromosome counts were obtained from flower buds fixed in alcohol and acetic acid (3:1); preparations were stained with acetocarmine.

In addition to the above, the following herbarium specimens were examined for morphological characters: KEDAH: Bongsu F.R., Symington 46982 (13 May 1938 flowers; KEP). – PERAK: Gunung Keledang, Ridley 9718 (Sept. 1898 flowers and fruits; SING, holotype!); Keledang [or "Kelidang"] Saiong F.R., Sow 33607 (02 Feb. 1934 fruits; KEP, SING), Symington 24473 (14 Nov. 1930 flowers; KEP, SING), 25596 (26 April 1931 flowers, KEP), 25760 (27 March 1931 fruits, KEP); Gunung Raya, Sow 47157 (19 June 1938 flowers; KEP); Gunung Korbu Peak, Symington 31410 (20 July 1933 flowers; KEP). – JOHOR: H.S. Labis, Sg. Marong, Wong FRI 32466 (26 May 1986 flowers; KEP).

Comparative investigations of "*Perakanthus*" (*Canthium*) *pauciflorus* were carried out on the type specimens of that species (*Scortechini* 62; 3 sheets in SING under Herb. Hort. Bot. Sing. nos. 67298, 67299 and 67300).

THE CHARACTER STATES OF *PERAKANTHUS*

MORPHOLOGY

Habit (Fig. 1A). *Perakanthus* is a monocaul treelet reaching a height of 4 m at the most. The solitary main stem produces paired, decussate, unbranched lateral axes which are held either ± horizontally, or ± ascending, or ± drooping.

On the lateral branches, the leaf pairs are all arranged horizontally (i.e. in one plane and not in decussate arrangement), and inflorescences are produced in the axils of these foliage leaves (Fig. 1B). In habit and architecture, *Perakanthus* thus resembles various other local Rubiaceae, notably *Lasianthus*.

The branches and at least the younger parts of the stems are (as virtually all other parts of the plant) densely beset with relatively long, white hairs, i.e. velvety hairy (for hair structure see Leaf and Hair Anatomy, further below).

Leaves and stipules. The leaves have short, velvety hairy petioles, ca. 3–5(7) mm long. The chartaceous to thinly coriaceous blades are ovate to elliptic, (4–)7–20 × (2–)2.5–7(–8) cm,

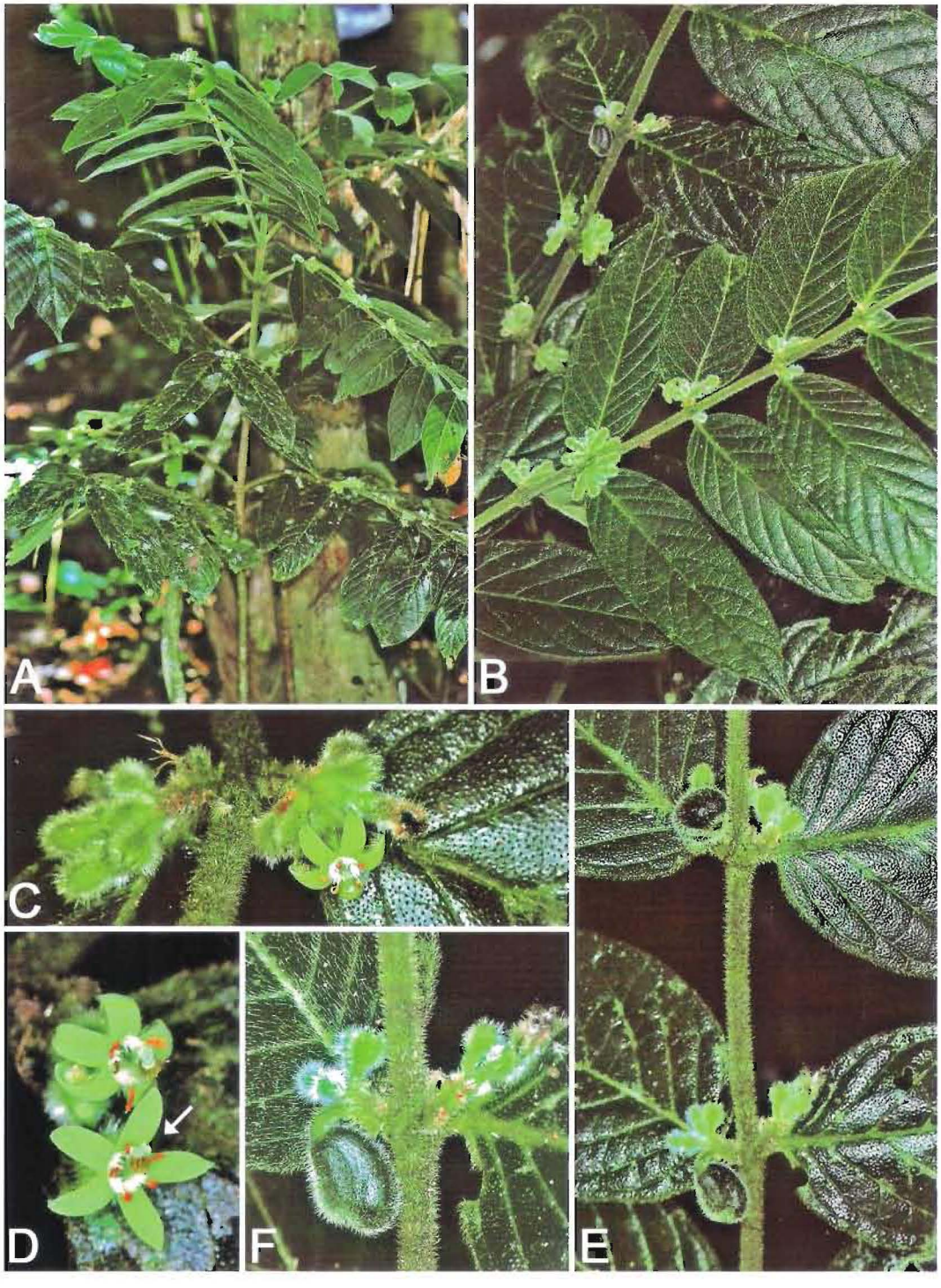

Fig. 1. *Perakanthus velutinus*. **A.** Habit. **B.** Branches with axillary inflorescences. **C.** Paired inflorescences in bud and with open flower. **D.** Open flowers in functionally female stage (arrow points to divergent stigma lobes). **E.** Two nodes with fruits. **F.** Fruit (left carpel aborted and smaller). All photos C. Puff (voucher *Zahid* et al. ZMS 31).

acute at the apex and rounded at the base, and have ca. 7–12 pairs of (± depressed) secondary veins. Blades are densely covered with white, spreading hairs (velvety hairy) at least on the lower surface (the indumentum is often less dense on the upper surface, and the hairs are shorter).

The densely hairy **stipules** are triangular and have an apical awn-like appendage ca. 5–10 mm long.

Fertile region: inflorescences, buds and flowers (Fig. 1B–D, 2A). The inflorescences consist of dense, subsessile to shortly pedunculate clusters of few (2–3) to 6 shortly pedicellate flowers per leaf axil (Fig. 1B–C). The densely white hairy pedicels are ca. 2–5(–7) mm long at anthesis (they elongate slightly during fruit development). The buds and the 5-merous flowers, too, are densely white hairy on the outside.

Buds shortly before anthesis are 8–15 mm long, ± oblong in outline but slightly curved and ± swollen basally (cf. section, Fig. 4A).

The **calyx** consists of minute triangular lobes (Fig. 2A) which are difficult to discern as they are hidden amongst the dense indumentum of the flower.

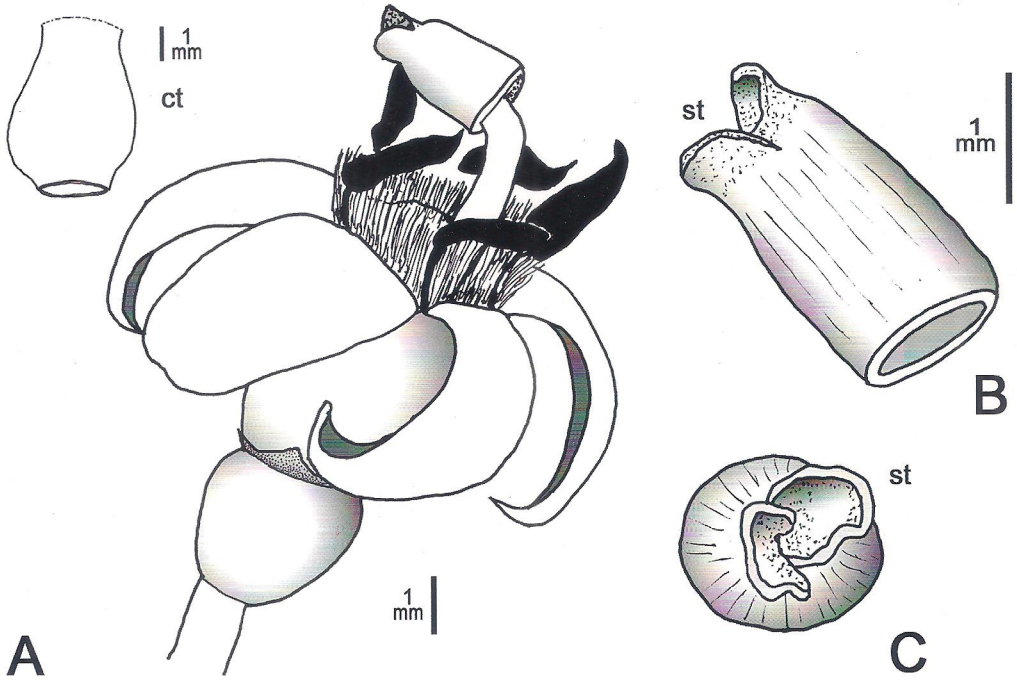

Fig. 2. *Perakanthus velutinus*. **A.** Flower (old and in functionally female stage; anthers shriveled up, stigma lobes diverging—see B–C) and detail of corolla tube (ct) to show its somewhat swollen (± bulbous) base and slight zygomorphy; the dense external indumentum (on ovary, calyx and corolla) is omitted. **B–C.** Stylar head complex (enlarged, cylindrical pollen collecting structure, receptaculum pollinis, below; stigma lobes, st, above) in side view and as seen from above. A–C Camera Lucida drawings from *Puff* 040402-1/1.

The green **corolla** has a tube 4.5–10(–12) mm long; the base of the tube is swollen (± bulbous), and the tube tends to be slightly curved (which may, however, not be very obvious, especially if a flower is rather short-tubed). The interior of the tube has a dense ring of long, unicellular hairs which point obliquely downwards, toward the style in the centre of the flower; their insertion point is around the upper end of the slightly swollen corolla tube portion (Fig. 4A). A second ring of dense hairs, also long and unicellular, but pointing upwards (i.e. erect), is at the throat and obscures the filaments. These throat hairs are white, contrasting with the green corolla (Fig. 1D, 2A).

The corolla lobes are valvate in bud and reflexed or ± spreading in open flowers; they are elliptic to ovate, ± acute at the apex and ca. 4–5 mm long. Their upper (inner) surface is smooth or, less commonly, beset with very short papillae.

The **stamens** are inserted at the throat, between the bases of the corolla lobes. The white filaments are ± as long as the hairs forming a ring at the throat or slightly longer (i.e. ca. 1 mm long). The (medi)basifixed oblong anthers have a length of ca. 2–2.5 mm; the connectives are apically drawn out into a short but distinct appendage (Fig. 4A: Ac).

The **gynoecium** consists of the small, subspherical inferior ovary, the style and what is commonly called "stigma"; the latter protrude from the throat for up to 7 mm.

The terminally borne mitriform structure ("stigma"), ca. 2.5–3 mm long, is better termed stylar head complex as it the bulk of it consists of enlarged, non-receptive stylar tissue; the actual receptive stigmatic areas are restricted to the apex and are made up of 2 lobes which diverge only in older flowers, being in a functionally female stage (Fig. 2B–C) [see Floral Anatomy and description of Secondary Pollen Presentation, further below, for further details].

The ovary is 2-chambered. Each locule has an apical placenta with a solitary, pendulous, anatropous ovule (Fig. 4A,C).

A ring-like nectariferous disk, surrounding the base of the style, sits on the roof of the ovary (Fig. 4A).

Fertile region: fruits and pyrenes; seed and embryo (Fig. 1E–F, 3). The shiny black, velvety hairy **drupaceous fruits** are borne on slightly thickened pedicels, elongated to ca. 1 cm. They are 12–15 × 8–12 mm, obovoid, slightly laterally compressed and didymous (if both carpels are fertile). Occasional abortion of one carpel results in a more irregular fruit shape (the fertile carpel becoming curved, growing around the smaller aborted carpel) (cf. Fig. 1F).

Inside the rather thin fleshy part of the fruit wall (i.e. the mesocarp) are the (typically) two woody **pyrenes**. They are 10–14 × 4–6 mm, compressed-ovoid, smooth and have a distinct dorsal ridge or keel and two lateral shoulders (Fig. 3A). If one carpel is aborted, the seed-containing pyrene usually is slightly curved.

The endocarp (forming the stone or pyrene) is thick, hard and sclerenchymatic, except for an area on the ventral side where the vascular bundle and placenta have originally entered the locule (cf. Fig. 3B, arrow). Upon slight exertion of pressure, the pyrene will split open apically (Fig. 3B, triangle). When the seed starts germinating, the radicle will emerge

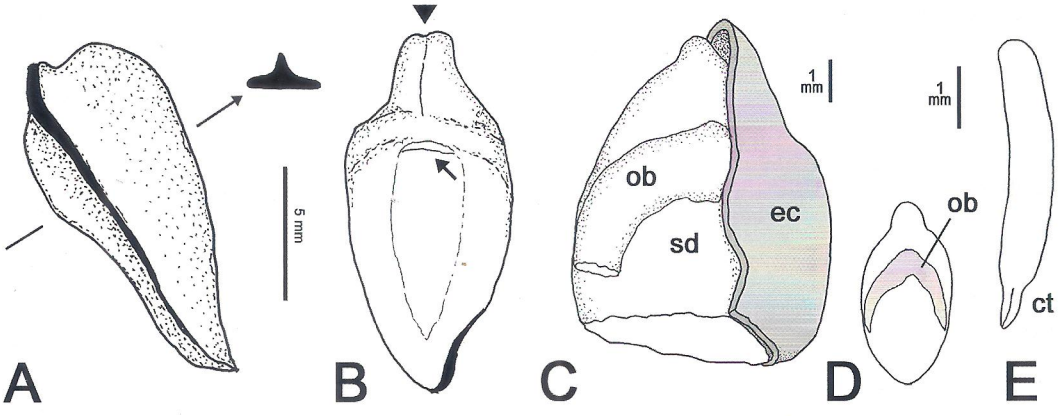

Fig. 3. *Perakanthus velutinus*. **A–B.** Pyrenes. **A.** View of dorsal side to show distinct keel (see schematic cross section). **B.** View of ventral side; the triangle at the top marks the area where the pyrene with break open when the seed starts to germinate; the arrow points to the thin-walled area where, in flowering stage, the placenta and its vascular supply entered the locule. **C.** Forcibly opened pyrene (upper part); pyrene wall (= stony endocarp, ec) removed on the left side to expose the seed (sd), note part of obturator (ob). **D.** Semischematic ventral view of seed showing the position of the crescent-shaped obturator (ob). **E.** Embryo, note very small cotyledons (ct). A–C, E Camera Lucida drawings from *Puff* 040402-1/1.

from this preformed "germination slit" (in general, common in Rubiaceae with pyrenes, but in many cases more elaborate than a mere split; cf. Robbrecht 1988 and Igersheim 1989 for examples from other members of the Vanguerieae).

The solitary **seed** contained in the pyrene has a very thin, hardly discernible exotesta. An estimated 90 % or more of its volume consists of endosperm. The small ± sausage-shaped embryo is long, thin and slightly curved; its cotyledons are small and indistinct. Within the seed, the embryo points upwards (as oriented in Fig. 3E) and thus points toward the preformed "germination slit" (see above).

A noteworthy feature of the seed is that it is ventrally covered by the persistent crescent-shaped obturator which extends down to the lower third of the seed (Fig. 3C–D). This is common in various members of the Vanguerieae (see illustrations in Igersheim 1989; obturator labeled as "strophiole"). See also Floral Anatomy: ovary, further below.

ANATOMY

Leaf and hair anatomy. The leaves of *Perakanthus* are thin (only about 1.25 mm thick) and hypostomatic. The blades have an upper epidermis whose cells are slightly thicker than those of the lower; the upper epidermal cells have rather thick outer walls and a thick cuticle. There is a single layer of elongated, cylindrical palisade cells, followed by a loose spongy mesophyll made up of rounded cells. A hypodermis is lacking, and tanniniferous cells seemed to be entirely absent in the investigated leaves.

The **hairs**, whose base is surrounded by a collar-like row of raised, elongated epidermis cells, are uniseriate and pluricellular ("septate hairs") ["cylindrical type" sensu Robbrecht

1988: 63, characterized by "individual cells not distinguishable on the straight outline of the cylindrical hairs" (as opposed to an "articulate type" whose pluri- or multicellular structure is recognizable by constrictions in the cross wall regions)]. Hair lengths as well as the number of cells making up a hair are variable (up to ca. 10 cells in some hairs, only 3–4 in others). The length of individual cells making up a hair, too, is variable. Hairs on the lower surface tend to be longer than those on the upper surface, but shorter hairs are often mixed with longer ones.

The same type of hairs is also found on all other external parts of the plants, including floral parts (ovary, calyx and outside of corolla; cf. Fig. 4) ("*external indumentum*" sensu Robbrecht 1988).

The "*internal indumentum*", on the other hand, invariably consists of unicellular hairs with a distinctly sculptured (rather than smooth) surface. It is restricted to the hair ring at the corolla throat and that at the upper end of the slightly swollen base of the corolla tube (Fig. 4A; see also Floral Morphology, above). This is consistent with the situation in most Rubiaceae (Verdcourt 1958, Robbrecht 1988).

Floral anatomy, with special reference to secondary pollen presentation and gynoecium. *Perakanthus*, like all other members of the tribe Vanguiereae, is characterized by flowers which show secondary pollen presentation, i.e., pollen is not presented to the pollinator by the anthers themselves but by a secondary structure (cf. Igersheim 1993, Puff et al. 1996).

Floral anatomy helps explain the situation in *Perakanthus* and makes clear the function of the most striking feature of genus, its stylar head complex (Fig. 4A–B and Fig. 2). It corresponds to the modified uppermost part of the style which, apically, incorporates the actual stigmatic surfaces. The swollen, ± cylindrical area below the actual stigmas serves as "receptaculum pollinis" (pollen receptacle, i.e. the organ on which the flower's own pollen is deposited, and which presents the pollen to the pollinator). As can be seen from the section of a bud shortly before anthesis (Fig. 4A), this structure is in close proximity to the anthers whose pollen sacs, at this stage, are ready to dehisce and will shortly deposit the mature pollen on to it (consequently, the flowers at this developmental state are functionally male; or, in other words, flowers are *protandrous*).

This "stylar head/receptaculum pollinis" forms a hollow cylinder in its basal part (due to collar-like downward growth, as documented by developmental studies by Igersheim 1993). Its surface is made up of enormously enlarged and elongated epidermal cells which are arranged parallel to each other and perpendicular to the surface (these cells are so large that they are clearly discernible even at relatively low magnification and show up as long, narrow, cylinders). The epidermal cells, moreover, have conspicuous ring-like thickenings in their distal parts, parallel to (and immediately below) the outer tangential walls (see Igersheim 1993 for the possible function of these thickenings). The subepidermal layers of the "stylar head/receptaculum pollinis" consist of rather dense tissue of small cells; a round, central core (with vascular bundles supplying the stigmas as well as with pollen transmitting tissue) is clearly discernible (see cross section, Fig. 4B).

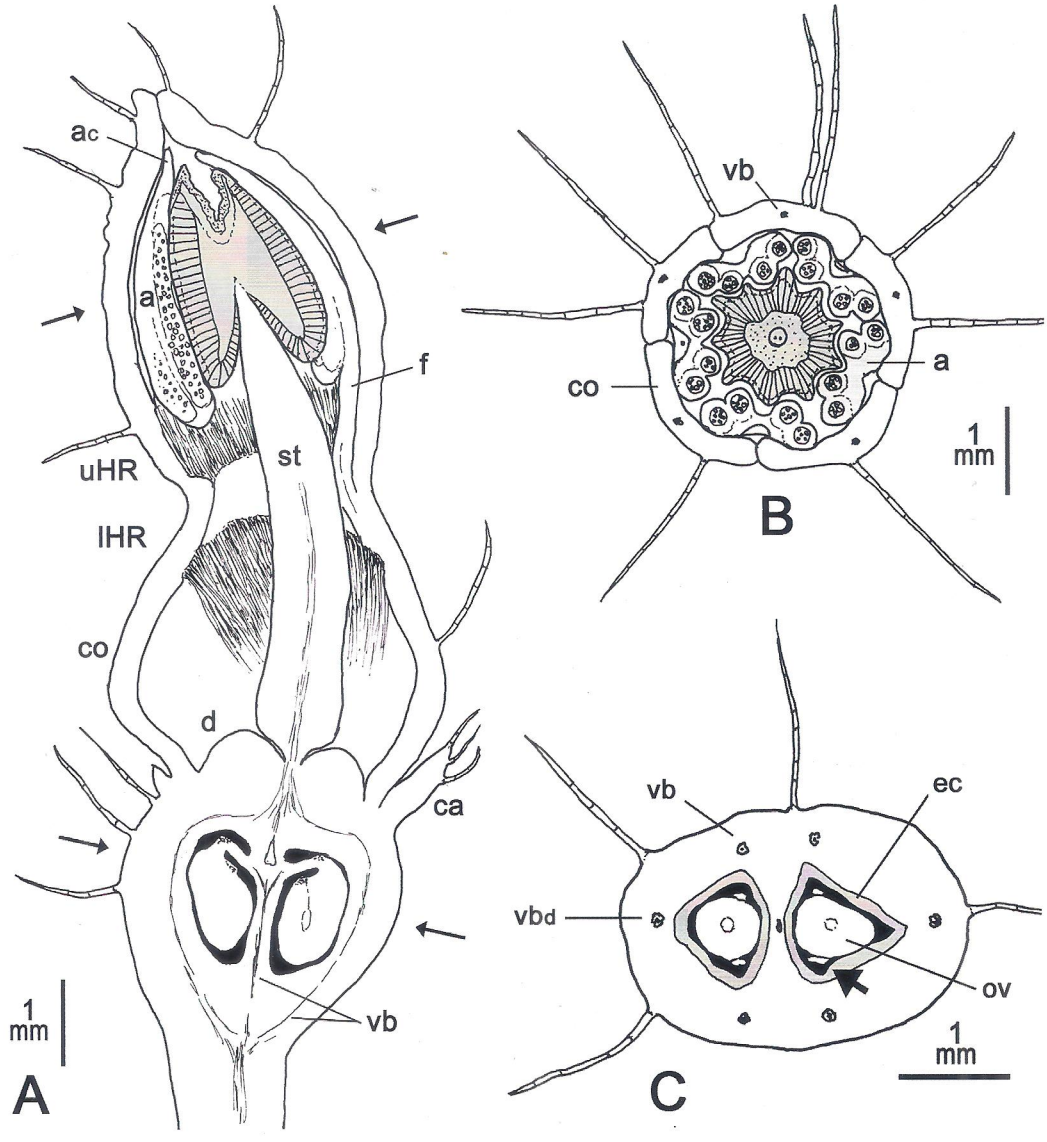

Fig. 4. *Perakanthus velutinus*, bud shortly before anthesis. **A.** Longitudinal section; upper and lower pair of arrows indicate the level where cross sections B and C, respectively, were made. **B.** Cross section to show position of the anthers and their pollen sacs in relation to the ridged stylar head complex (shaded grey). **C.** Cross section of ovary; the arrow points to one of the obturator lobes. Abbreviations: a, anther (ac, apical anther connective appendage in A); ca, calyx lobe; co, corolla tube (A) or lobe (B); d, nectariferous disk; ec, developing endocarp (shaded grey); f, filament; ov, ovule; st, style; vb, vascular bundle (vbd, dorsal vb of one of the two carpels); lHR, uHR, lower and upper internal hair ring. The dense external indumentum is reproduced incompletely (only a few selected hairs are drawn to show their characteristics). Further explanations in the text. A–C Camera Lucida drawings of hand and microtome sections; all from *Puff* 040402-1/1.

Cross sections reveal that the "stylar head/receptaculum pollinis" is distinctly 10-rigded, with the raised areas extending into the recessed areas of the pollen sacs of the 5 anthers (Fig. 4B). At a slightly later bud stage than depicted here, i.e. after the pollen sacs have dehisced, its entire surface will be densely packed with mature pollen.

The actual stigmatic areas, appearing V-shaped in longitudinal section, consist of unicellular ± globose to obovoid stigmatic (receptive) papillae. At late bud stage, their (not yet) receptive surfaces invariable face inward (i.e. towards the imaginary central axis in the longitudinal section) and never can come in contact with the anthers (which, in the uppermost part, are sterile and only possess connective appendages; see section, Fig. 4A).

As a flower passes from its functionally male to its functionally female stage (some time after anthesis), the stigmatic lobes (with their by now *receptive* papillae) start to unfold and enlarge somewhat (see Fig. 2A–C and Fig. 1D, arrow).

Detailed anatomical investigation of the **gynoecium** also reveals the following noteworthy features:

The style (below the stylar head complex) is rather thick and "stocky". Its surface is totally smooth. This deserves mentioning because in many other Vanguerieae it is beset with hairs; cf. Igersheim (1989). Its central core contains pollen transmitting tissue and small vascular bundles running upwards to supply the stigmas.

The bicarpellate ovary has a rather thick wall and, even in bud shortly before anthesis, several layers of dense, small cells coating the locules are discernible (Fig. 4C). These are the initial stages of the endocarp which, in fruiting stage, will form the stony pyrene wall. The "typical" vascularization is recognizable in cross section: a main dorsal and a pair of lateral bundles per carpel (Fig. 4C); both cross and longitudinal section show that there is also a main bundle in the central part of the septum which will fork apically to enter the placentas.

A distinct obturator is developed in the area of the micropyle of the anatropous ovules. This obturator extends downward on either side of an ovule (see section, Fig. 4C). Rather than deteriorating after fertilization it persists and even enlarges after fertilization and is visible as a crescent-shaped structure on the ventral side of mature seeds (see also Seeds, above).

PALYNOLOGY

Based on light microscopical investigations, pollen grains of *Perakanthus* are suboblate, 3-porate and 40–50 × 56–62 µm. The sexine is perforate, with very small, hardly detectable perforations.

KARYOLOGY

A chromosome count [voucher *Puff* 040402-1/1] obtained from young flower buds (pollen mother cells meiosis) yielded n=22. *Perakanthus*, thus, is a tetraploid on a basic number of x=11.

DISTRIBUTION AND ECOLOGY (Fig. 5)

Perakanthus is endemic to the Malay Peninsula and apparently very rare. It is only known from about a dozen collections from five localities, one from southern Kedah, three from Perak and one from Johor. The first 4 localities are all ± close together, whereas the "southern" Johor locality is more isolated geographically (see also intraspecific variation, below).

Ecological information (incl. altitudinal data) is sparse, but it would seem from the general nature of the known localities that lower montane and lowland forest are the preferred habitats.

Phenology: Flowering material is known from April to July, September, November and December; fruiting specimens from February to April.

A NOTE ON INTRASPECIFIC VARIATION

The "northern" collections of *Perakanthus* are relatively uniform (except for expected variation in leaf sizes and shapes and density of the external indumentum); the few flowering collections have flowers with relatively long corolla tubes, their lengths ranging from about 8 to 10 (and sometimes 12) mm. They correspond to those depicted by Robyns (1928 : fig. 35 and 36D–E).

In the only known "southern" (Johor) locality, the two known collections (possibly from roughly the same site) are characterized by having relatively short corolla tubes, always well below 8 mm and sometimes not more than 4.5 mm long. Although short, the corollas agree with those from "northern" collections in having a slightly swollen base and in being faintly zygomorphic. In all other respects, "northern" and "southern" specimens are indistinguishable.

In view of the very few collections available of the species, we refrain at this stage from formally recognizing this difference as variety or, possibly, geographical subspecies.

DISCUSSION

Perakanthus sensu Robyns (1928) – a "mixed bag"

When dealing with *Perakanthus*, Robyns (1928: 330–331) provided the following brief and rather non-descript diagnosis for the new genus [as Robyns' entire publication was written in Latin, this and all the following quotes and citations are translations]: Shrubs with always opposite, petiolate leaves; flowers large, solitary or in groups of 2(–3); corolla slightly

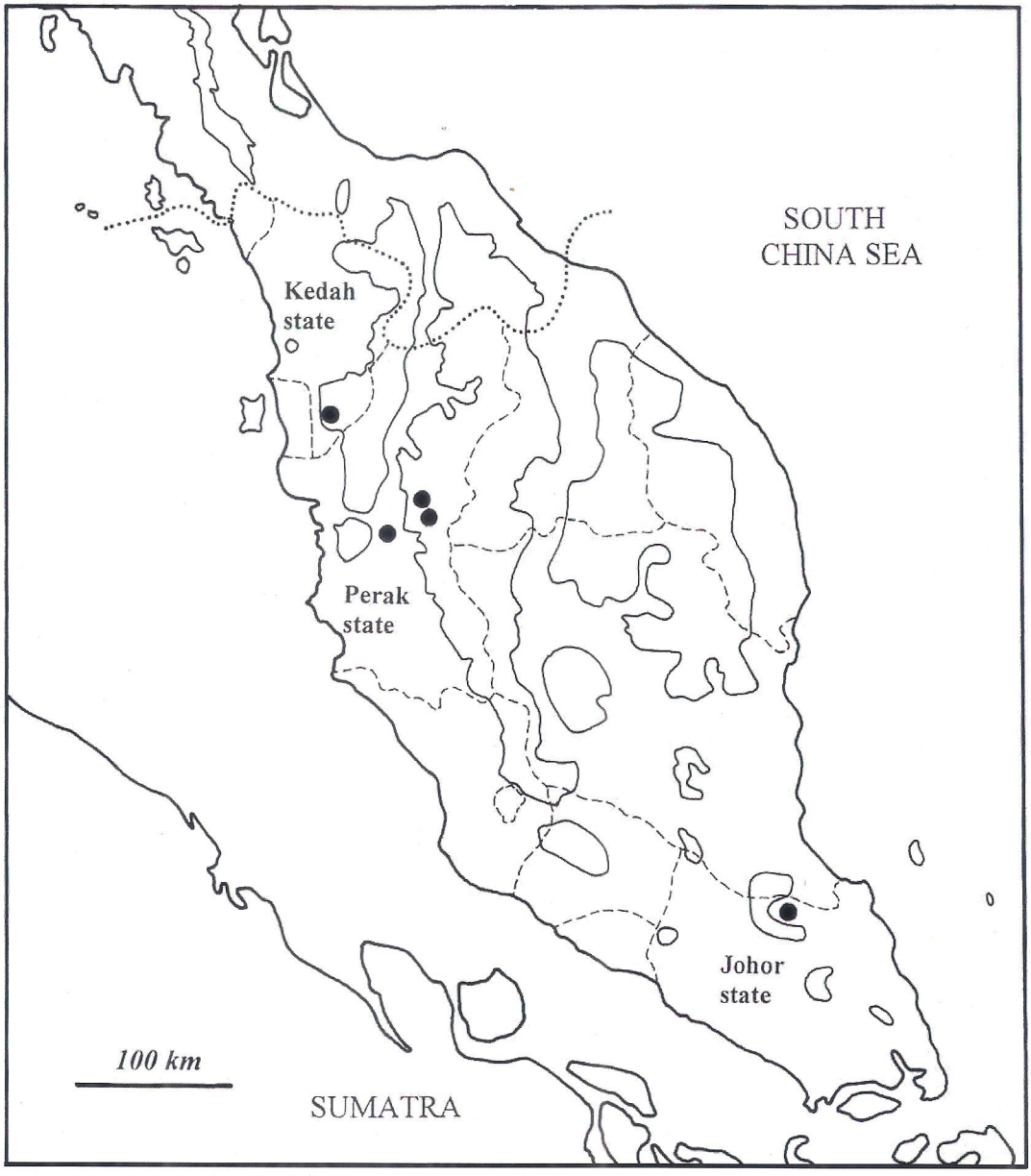

Fig. 5. Known distribution of *Perakanthus velutinus* (represented by dots) in three states in Peninsular Malaysia. Solid lines within the peninsula demarcate areas above 500 m. Dotted line represents boundary with Thailand in the north, dashed lines are state boundaries.

curved, glabrous or pilose on the outside; stigma mitriform, with the apex distinctly 2-lobed; ovary bilocular.

This was followed by a more detailed generic description and a sentence saying that two species were known to him, both from the Malay Peninsula (Perak). The two species were then keyed out, and *"Perakanthus" pauciflorus* was distinguished from *Perakanthus velutinus* in being an entirely glabrous shrub, in having ovate-elliptic, coriaceous, leaves with petioles 5–8 mm long, solitary glabrous flowers and glabrous fruits.

The two species were not described separately in his publication, presumably because the characters known to him were already included in the generic description. There is only a short taxonomic section in which the necessary new combinations were made (as both had originally been described as *Canthium* species) and in which the investigated specimens were listed (one—the type—for *"Perakanthus" pauciflorus*, and two—including the type—for *Perakanthus velutinus*). A type species for the genus was not indicated.

Reinvestigation of *"Perakanthus" pauciflorus* (by Wong, when preparing his Rubiaceae account for Tree Flora of Malaya: Wong 1989, and during the current study), which included a number of characters not dealt with by Robyns (l.c.), revealed several fundamental character state differences from *Perakanthus velutinus* while it, on the other hand, uncovered many agreements with *Canthium* (*sensu lato*):
"Perakanthus" pauciflorus has paired short shoot thorns ("spines") on the long shoots, as is typical for a number of *Canthium* species known from the Malay Peninsula (and elsewhere). King & Gamble (1904: 58–59) had clearly characterized their new species (as *Canthium pauciflorus*) as "a spiny glabrous shrub…", yet Robyns (l.c.) in his "mixed bag" generic description of *Perakanthus* wrote: "Erect shrubs, mostly unarmed…".

The inflorescences of *"Perakanthus" pauciflorus* are basically axillary, however not in the axils of long shoot leaves (as in *Perakanthus velutinus*) but in the axils of reduced leaves on lateral, contracted short shoots. This, in the Malay Peninsula and neighbouring areas, is characteristic for some taxa of *Canthium* and also for the closely allied *Meyna*. The individual flowers of a fascicle are, moreover, subtended by a pair of fused bracts which is immediately below the ovary (Fig 6A).

The flowers of *"Perakanthus" pauciflorus* and *Perakanthus velutinus* agree in being relative large (corolla tubes to about 10 mm long), but those of *"Perakanthus" pauciflorus* differ not only in being glabrous on the outside but also in the following features:

(1) The corolla tubes are straight and cylindrical and do not show even a faint curvature. The interior of the corolla differs in lacking a ring of stiff, erect hairs at the throat; there is only a ring of long, deflexed hairs in the lower half of the corolla tube (Fig. 6). Such an internal indumentum is known, for example, from some African species of *Canthium*, *Psydrax* and *Keetia* (cf. illustrations in Igersheim 1989).

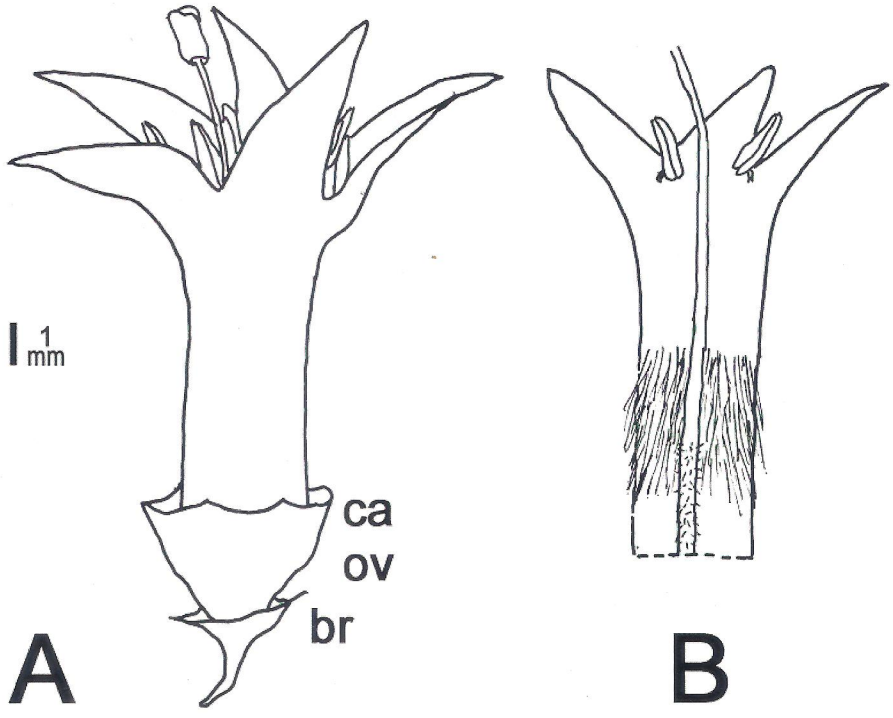

Fig. 6. *Canthium ["Perakanthus"] pauciflorum.* **A.** Flower subtended by a pair of bracteoles (br; ov, ca: inferior ovary and cupular calyx). **B.** Corolla tube opened to show ring of deflexed hairs; also note short hairs on basal part of style. Camera Lucida drawings from *Scortechini* 62.

(2) Basally, the style is beset with short hairs, a character also known from various *Canthium* species and other members of the Vanguerieae (cf. Igersheim l.c.).

(3) The drupes of *"Perakanthus" pauciflorus* (typically) contain two pyrenes, each of which is ± flat on the ventral and convex on the dorsal side. Pyrene shape thus largely corresponds to that found in *Canthium sensu lato* (although the ventral pyrene side is more often ± concave rather than entirely flat). In any case, it strikingly differs from pyrenes of *Perakanthus velutinus* which are characterized by a distinct dorsal keel.

In summary, these differences strongly discourage the placement of these two species into one and the same genus. In view of character state agreements between *"Perakanthus" pauciflorus* and *Canthium* (*sensu lato*), it seems to be the most reasonable solution at this stage to transfer the species back to its original position, *Canthium pauciflorum*, as already suggested by Wong (1989: 390). Bridson (1992) indicated her agreement by placing the species in her informal "Group II" of *Canthium sensu lato*.

Consequently, Robyns' (1928: 330) generic description of *Perakanthus* needs to be formally emended to exclude the characters of *"Perakanthus" pauciflorus*.

***Perakanthus* Robyns (1928) emend. Wong & Puff**

Unarmed, velvety hairy monocaul treelets with petiolate, opposite leaves in one plane on lateral branches. Inflorescences paired, in the axils of long shoot leaves. Flowers 5-merous, densely hairy outside, in fascicles of few (2–3) to 6. Corolla green, tube with basal swelling, slightly curved (zygomorphic), inside with a ring of deflexed hairs at upper end of slightly swollen part of tube and with a ring of erect hairs at the throat. Stamens inserted at throat, between the bases of the corolla lobes, filaments filiform, anthers (medi)basifixed, apically with short but distinct sterile connective appendage. Ovary inferior, 2-chambered, each locule with an apically attached, pendulous solitary ovule; lower part of style thick and glabrous, above modified into a mitriform stylar head complex, apically bearing two stigma lobes. Fruits drupaceous, didymous (if both carpels are developed); pyrenes compressed-ovoid, smooth, with a distinct dorsal ridge or keel and two lateral shoulders; each pyrene with a solitary seed.

Only species: *Perkanthus velutinus* (Ridl.) Robyns in Bull. Jard. Bot. Etat Brux. 11: 331 (1928).
Basionym: *Canthium velutinum* Ridl. in J. Straits Branch Roy. Asiatic Soc. 61: 19 (1912).
Type: Perak, Gunung Keledang, Sept. 1979, *Ridley* 9719 (SING, holo.!).

Note. Robyns' typification was incorrect. Under *Perakanthus velutinus*, he listed two specimens: "Perak, ad locum Hermitage nominatum, Dec. 1884, *Curtis* 1339", and the above *Ridley* specimen. For reasons unknown, he, however, marked the *Curtis* collection as the type, although this specimen had not even been cited in Ridley's original publication.

Robyns' (1928) ideas on the relationship and affinities of *Perakanthus*

In his "graphic presentation of generic affinities", Robyns (1928: fig. 2) placed *Perakanthus* and the two African genera *Temnocalyx* and *Ancylanthos* (as "*Ancylanthus*"; see following note) in his "subgroup Ancylanthos." [Note: As pointed out by Verdcourt & Bridson (1991: 800), Robyns, l.c., by mistake (or unnecessarily) changed the spelling of *Ancylanthos* Desf. to "*Ancylanthus*"; the correct spelling is used throughout the current text].

This presumed "alliance" between the two African genera and *Perakanthus* was essentially based on a single character, as can be seen from his general key, in which he distinguished these three genera from the remainder of the Vanguerieae in the following way:
"Corolla tube curved, wide and elongated" [vs. "Corolla tube always straight, mostly short, sometimes elongated and very narrow"]. In the following key sections, he distinguished *Perakanthus* from the two African genera by having a 2-locular ovary [vs. 3-5-locular] and a mitriform stigma with a 2-lobed apex [vs. "cylindrical or rarely coroniform stigma"], and always opposite leaves.

Probably due to the lack of sufficient material available to him at the time, and because many character states were not studied in detail, he left it at that and did not elaborate further.

From a present-day point of view, both the recognition of a "subgroup Ancylanthos" and the assumed affinities within this alliance appear rather "thin" and are based on few technical characters. Moreover, the definition of subgroup, merely held together by superficially similar large, slightly zygomorphic flowers, was not even fully correct (*"Perakanthus" pauciflorus* does not have curved corollas! See the previous subchapter).

Comments on the status of *Perakanthus* and its position within the Vanguerieae, based on currently available data

The Vanguerieae are an Africa and Madagascar-centred tribe consisting of 27 genera (Lantz & Bremer 2004). In addition to *Perakanthus*, the genera *Canthium*, *Psydrax*, *Pyrostria* and *Meyna* are generally recognized in Asia, but most of them are ill-known and need revision. Their generic circumscription, moreover, is unclear and not yet satisfactorily resolved.

According to Bridson (1992) *Canthium sensu stricto* is restricted to Africa except for two species from India and Sri Lanka, respectively; Asiatic species of *Canthium sensu lato* were divided into various groups which may represent undescribed genera. Detailed research on these has, however, never been carried out. When reinstating *Psydrax* (Bridson 1985), she implied that many Asiatic taxa currently placed in *Canthium* also need to be transferred. These transfers have formally been made for Sri Lankan taxa (Ridsdale 1996, 1998); for the Malay Peninsula (Wong 1989) several (mostly unnamed) *Psydrax* species have been recognized. Elsewhere in continental Asia (Thailand, Indochina), *Psydrax* is either still "hidden" in *Canthium* or only informally recognized as a distinct genus in floras and the like (e.g. Puff et al. 2005).

Redelimitation of *Pyrostria* resulted in a massive expansion of the genus and, within *Pyrostria sensu lato,* an Afro-Madagascan and an Asiatic group were distinguished (Bridson 1987). Several unisexual *Canthium* species (amongst them *C. cochinchinenis*, which also occurs in the Malay Peninsula) were listed as belonging to the latter group. No attempt, however, has ever been made to formally recognize these (either as a subgenus of *Pyrostria* or as a new genus allied to *Pyrostria sensu stricto*).

Lantz & Bremer (2004) reduced *Meyna* to a synonym of *Canthium*, based on molecular and morphological work on the African *Meyna tetraphylla*. As they have not investigated the Asiatic species (which are badly in need of revision) we, at present, do not accept that the ENTIRE genus should be sunk but provisionally maintain *Meyna*.

In view of all these problems, thoughts on the alliances and status of *Perakanthus* can only be of a very preliminary nature. The situation is complicated even further by the fact that many of the character states of *Perakanthus*, if compared one by one to those of other Vanguerieae (and especially Asiatic ones), are rather inconclusive, in that they are also known from selected taxa of other genera and not unique:

Floral characters. The slightly curved corolla tube with a somewhat swollen base and with its relatively large size is ± unique, but there are exceptions: in *Meyna*, the corolla tubes are sometimes a little swollen at the base, and *Canthium sensu lato* (*C. pauciflorum*!) can have relatively large corollas.

Internal indumentum as in *Perakanthus* (a ring of deflexed hairs within the tube plus an erect hair ring at the throat) is not precisely replicated in other Asiatic Vanguerieae, but there are various combinations which make if difficult to clearly distinguish the genus (*Canthium sensu lato*: ring of deflexed hairs in tube only, glabrous or pubescent at throat, entire tube pubescent inside or, rarely, ± glabrous altogether; *Psydrax*: corolla tube inside with ring of deflexed hairs or sometimes hairs not restricted to a well defined ring or absent, often pubescent at throat; *Meyna*: hairy at throat and with a ring of deflexed hairs inside, immediately below throat; *Pyrostria sensu lato*: hairy at throat, lacking well-defined ring of deflexed hairs inside tube).

The type of stylar head complex ("stigma") in *Perakanthus* [stigmatic (receptive) surfaces tightly pressed together in bud and throughout the functionally male stage of a flower; "Type 1 SH-Complex" sensu Igersheim 1993] is common in Vanguerieae and recorded, amongst others, for *Canthium*, *Psydrax*, *Meyna* and *Pyrostria* (cf. Igersheim 1989: Fig. 77). "Type 2 SH-Complex", in which stigmatic surfaces are exposed from quite early developmental stages, is confined to taxa restricted to Africa. Within the Asiatic Vanguerieae, *Psydrax* stands out in having the stylar head complex ("stigma") much longer exserted from the throat than in the other genera.

Most Vanguerieae, like *Perakanthus*, have hermaphrodite flowers. Within the tribe, dioecy (unisexual flowers) are only known from an African subgenus of *Canthium*, *Peponidum* (Madagascar-centred) and *Pyrostria sensu lato* (including the Asiatic informal "Group B" of Bridson 1987).

Fruit, seed and embryo. A truly unique character of *Perakanthus* is the unusual dorsally keeled pyrene. Such a pyrene shape is not recorded from any other Asiatic member of the Vanguerieae [although similar pyrenes are illustrated for *Cuviera* (cf. Verdcourt & Bridson 1991: fig. 132,27), a strictly African genus which differs markedly in other character states]. Seeds and embryos are, however, similar to those of many other Vanguerieae: Persistent obturators remaining attached to the seed have been illustrated for (African) *Canthium* and *Psydrax* (Igersheim 1989); they are possibly almost universally present but have hardly ever been documented as preparation is difficult. Embryos with the radicles much longer than the cotyledons are common in Vanguerieae and are recorded for *Canthium*, *Meyna*, *Psydrax* and *Pyrostria* (Igersheim 1989). Exceptions (radicle : cotyledon length 1 : 1 or <1 : 1) occur

only in some genera restricted to Africa and in some of those African *Canthium* species recently separated as *Afrocanthium* (Lantz & Bremer 2004).

Pollen. The sexine of *Perakanthus* pollen grains corresponds to "Type II" found in Vanguerieae (*sensu* Lens et al. 2000); it has been recorded in (African) *Canthium* and *Vangueria*. "Type I" occurs in (African) *Keetia* and *Psydrax*. Pollen grain shape (suboblate) is in agreement with many Vanguiereae, as is size (cf. Lens *l.c.*)

Chromosome number. The chromosome number of *Perakanthus* is in agreement with those of other members of the tribe Vanguerieae. Of the investigated 12 genera and 35 taxa of the tribe, all but one somewhat doubtful count from Africa yield tetraploid numbers on a basic number of x=11 (Kiehn 1995). The majority of counts originate from Africa, but a few species of *Canthium* [*sensu lato*] from India were also investigated (data summarized in Kiehn 1986). Karyology, thus, also cannot provide useful clues to the taxonomic position of the genus.

Leaves and leaf anatomy. Thinnish leaves are not only typical of *Perakanthus* but are also characteristic of Asiatic *Canthium sensu lato* and *Meyna*. In the latter two genera, leaves can either be glabrous or hairy. The remaining Asiatic Vanguerieae, *Psydrax* and *Pyrostria sensu lato* tend to have leathery leaves which are mostly glabrous.

Tilney et al. (1990) demonstrated that leaf anatomical characters of [southern African] *Canthium sensu lato* (i.e. *Canthium sensu stricto*, *Psydrax* and *Keetia*) can be of taxonomic significance at the species level. At the generic level, however, characters are no longer fully consistent, although a distinction is still possible. Taking, for example, presence / absence of tanniniferous deposits in the leaf tissues, it was found that, in the investigated taxa, they were generally absent in *Psydrax*, generally present in *Keetia* but either present or absent in *Canthium*. Absence of tannins in *Perakanthus* leaves, thus, is not an unambiguous character.

From the above, the following can be concluded:
A closer association of *Perakanthus* with both *Pyrostria sensu lato* and *Psydrax* can be excluded with a high degree of certainty: the former primarily on account of its unisexual flowers, the latter primarily because of its often distinctly leathery leaves, its long style which lifts the stylar head complex ("stigma") high above the level of the throat and its often reflexed anthers.

Relationships of *Perakanthus* with the two remaining "candidates", *Canthium sensu lato* and *Meyna*, are much more difficult to assess. Under the assumption that *Meyna is* generically distinct from *Canthium*, a possible alliance with *Perakanthus* can be discounted on account of *Meyna's* 4–5-carpellate ovary, its occasionally 3-whorled leaves and the presence of axillary "spines" (short shoot thorns). That leaves *Canthium sensu lato* as the only genus complex, to which *Perakanthus* may have a close alliance.

At present it does not seem possible to assess with certainty if the status of *Perakanthus* as a monotypic genus is warranted or not. Some arguments in favour of a generic status may be brought forward (velvety hairy appearance; characteristic pyrenes) but in view of the ill-known state of the *Canthium* complex in Asia, these may not hold.

It may, thus, be the best solution to leave the status of *Perakanthus* as a monotypic genus untouched at this stage and to encourage detailed investigations (including molecular studies) of the complex *Canthium* group in Asia which could shed new light on the position and relationships of the genus.

REFERENCES

Bridson, D.M. (1985) The reinstatement of *Psydrax* (Rubiaceae subfam. Cinchonoideae, tribe Vanguerieae) and a revision of the African species. *Kew Bull.* 40: 687–725.

Bridson, D.M. (1987) Studies in African Rubiaceae-Vanguerieae: a new circumscription of *Pyrostria* and a new subgenus, *Canthium* subgen. Bullockia. *Kew Bull.* 42: 611–639.

Bridson, D.M. (1992) The genus *Canthium* (Rubiaceae-Vanguerieae) in tropical Africa. *Kew Bull.* 47: 353–401.

Igersheim, A. (1989) Beiträge zur Klärung der Gattungsabgrenzungsprobleme innerhalb der Rubiaceae-Vanguerieae. Unpublished PhD Thesis, Form.-Naturwiss. Fak., Univ. Wien. 241 pp.

Igersheim, A. (1993) Gynoecium development in Rubiaceae-Vanguerieae, with particular reference to the "stylar head"-complex and secondary pollen presentation. *Pl. Syst. Evol.* 187: 175–190.

Kiehn, M. (1986) Karyologische Untersuchungen und DNA-Messungen an Rubiaceae und ihre Bedeutung für die Systematik dieser Familie. Unpublished PhD Thesis, Form.-Naturwiss. Fak., Univ. Wien. 225 pp.

Kiehn, M. (1995) Chromosome survey of the Rubiaceae. *Ann. Missouri Bot. Gard.* 82: 398–408.

King, G. & J.S. Gamble (1904) Materials for a flora of the Malayan peninsula. No. 15. *J. Asiatic Soc. Bengal 73, part 2 - Nat. Sc.*: 47–135.

Puff, C., Chayamarit, K. & V. Chamchumroon (2005). Rubiaceae of Thailand. A pictorial guide to indigenous and cultivated genera. The Forest Herbarium, National Park, Wildlife and Plant Conservation Department, Bangkok. 245 pp.

Puff, C., Robbrecht, E., Buchner, R. & P. De Block (1996) A survey of secondary pollen presentation in the Rubiaceae. In: E. Robbrecht, C. Puff & E. Smets (ed.), Second International Rubiaceae Conference, Proceedings. *Opera Bot. Belg.* 7: 369–402.

Ridsdale, C.E. (1996) New taxa and combinations for the Rubiaceae of Sri Lanka. *Blumea* 41: 455–462.

Ridsdale, C.E. (1998) Rubiaceae. In: M.D. Dassanayake (ed.), A revised handbook to the Flora of Ceylon, Vol. 12. Amerind Publ. Co. Pvt. Ltd., New Delhi. Pp. 141–343.

Robbrecht, E. (1988) Tropical woody Rubiaceae. *Opera Bot. Belg.* 1: 1–271.

Robyns, W. (1928) Tentamen monographiae Vanguerieae generumque affinium. *Bull. Jard. Bot. Etat Brux.* 11: 1–359.

Lens, F., Jansen, S., Huysmans, S., Robbrecht, E. & E. Smets (2000) Pollen morphological variation in Vanguerieae (Ixoroideae-Rubiaceae). *Grana* 39: 90–102.

Lantz, H. & B. Bremer (2004) Phylogeny inferred from morphology and DNA data: characterizing well-supported groups in Vanguerieae (Rubiaceae). *Bot. J. Linn. Soc.* 146: 257–283.

Tilney, P.M., Kok, P.D.F. & A.E. Van Wyk (1990) The taxonomic significance of anatomical characters of the leaf in the Southern African species of *Canthium* s.l. (Rubiaceae). *S. Afr. J. Bot.* 56: 363–382.

Verdcourt, B. (1958) Remarks on the classification of the Rubiaceae. *Bull. Jard. Bot. Etat Brux.* 28: 209–281.

Verdcourt, B. & D. Bridson (1991) Rubiaceae (part 3). In: R.M. Polhill (ed.), Flora of Tropical East Africa. A.A. Balkema, Rotterdam, Brookfield. Pp. 749–956.

Wong, K.M. (1989) Rubiaceae. In: F.S.P. Ng (ed.), Tree flora of Malaya, Vol. 4. Longman Malaysia, Petaling Jaya. Pp. 324–425.